

Mortality of Young Brown Shrimp *Penaeus aztecus* in Estuarine Nurseries

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Abstract.—We estimated actual 2-week mortalities of postlarval and juvenile brown shrimp in a Galveston Bay salt marsh by comparing densities of cohorts throughout the spring. Mortalities ranged between 33% and 61% in 1982 and 23% and 39% in 1987. Brown shrimp mortality in predator-exclusion cages during 1987 was less than 3%. These data and published information on food requirements, diseases, and physical tolerances suggest that predation is usually the major direct cause of brown shrimp mortality in estuarine nurseries of the northern Gulf of Mexico. Southern flounder *Paralichthys lethostigma* was the dominant fish predator on brown shrimp during the spring, and appeared to be responsible for a large portion of brown shrimp mortality. In laboratory experiments, the presence of smooth cordgrass *Spartina alterniflora* reduced predation rates of southern flounder and some of the other fish predators examined. Predation rates in general increased in proportion to increased prey densities. Thus, low water levels in the marsh, which reduce access by brown shrimp to intertidal vegetation and increase their densities on nonvegetated bottom, probably result in increased brown shrimp mortality. Mortality and growth may also interact, and predation pressure should be reduced as brown shrimp grow and exceed optimal prey size. Indeed, mortality in the marsh appeared to decline as brown shrimp size increased.

The number of brown shrimp recruited to the fishable population each year is ultimately controlled by spawning success and by mortality of prerecruits. There is little evidence for recruitment overfishing or for a strong spawner-recruit relationship in the Gulf of Mexico fishery (Nance and Nichols 1988); thus mortality of young brown shrimp appears important in regulating recruitment success. Year-class strength will be determined primarily during life cycle stages when mortality rates are large and variable. Accordingly, research on recruitment processes should be focused on these critical life stages.

Spawning and larval development of brown shrimp occurs in waters over the continental shelf (Cook and Lindner 1970). Postlarvae (10–15 mm, total length) enter the bays in large numbers throughout the spring and migrate to shallow and often vegetated nursery areas (Baxter and Renfro 1967; Zimmerman et al. 1984). When juveniles reach a size generally greater than 55–60 mm, they move into the open bays and become available to the inshore fishery (Baxter et al. 1988). The subadults then migrate into the coastal waters where they are exploited by the offshore fishery.

Brown shrimp are typically spawned and harvested within the same year, and correlations of abundance at different periods in their life cycle may be useful in identifying critical stages that regulate recruitment success. Klima et al. (1982,

1987) and Baxter and Sullivan (1986) have demonstrated a strong correlation between the catch of bait-size brown shrimp (approximately 60–100 mm) in Galveston Bay, Texas, and annual offshore landings. This relationship indicates that mortality and growth is low or constant in the later life stages, and that year-class strength is fixed before brown shrimp leave estuarine nurseries. This conclusion is supported by relatively low estimates of natural mortality in adult populations (see Rothschild and Brunenmeister 1984 for review) and the apparent lack of predation on brown shrimp in coastal waters (Divita et al. 1983; Sheridan and Trimm 1983; Sheridan et al. 1984).

Efforts to correlate the abundance of postlarvae entering bays with subsequent offshore landings have generally been unsuccessful (Berry and Baxter 1969; Ford and St. Amant 1971; Baxter and Sullivan 1986). In large part this may be due to the difficulty in obtaining accurate abundance estimates during a period when the population is migrating through passes and entering the bays. However, Sutter and Christmas (1983) sampled in shallow areas within a bay system, and abundances of postlarvae still did not correlate well with offshore catch. Thus, the number of postlarvae entering estuaries appears to only partially explain variability in recruitment of brown shrimp to the fishery, and mortality of the young in estuarine nurseries appears critical in fixing recruit-

ment levels. Predation by fishes during this period in estuaries may be a primary cause of brown shrimp mortality. In contrast to studies conducted in offshore waters (Divita et al. 1983; Sheridan and Trimm 1983), analyses of fish stomach contents have shown that young penaeid shrimp are frequently eaten by estuarine fishes (see Minello and Zimmerman 1983 for review). Our objectives were to measure brown shrimp mortality in a Galveston Bay salt marsh and to determine whether predation by fishes was an important cause of this mortality. Overall, the research was designed to increase our understanding of processes regulating brown shrimp mortality in estuarine systems.

Methods

Mortality estimates.—We measured densities of postlarval and juvenile brown shrimp in the spring of 1982 and 1987 in a salt marsh on the West Bay side of Galveston Island, Texas. This marsh is a reticulated complex of shallow nonvegetated bottom (<1 m in depth) and patches of smooth cordgrass *Spartina alterniflora*. A detailed description of the marsh location, drop-sampling technique, and sampling methods is given in Zimmerman et al. (1984). The technique basically involves dropping a 1.8-m-diameter cylinder from the bow of a skiff and removing enclosed fauna with a pump and dip nets.

At 2-week intervals on flood tide, we collected an equal number of samples in both *Spartina alterniflora* habitat and on nonvegetated bottom. In 1982, 24 samples were collected during each sampling period (representing 62 m² of marsh area); in 1987, 20 samples were collected (52 m²). The mean density (represented as brown shrimp/100 m²) from all samples collected during each period was considered to represent the population in the marsh complex (about 4 km² in area).

Total length (tip of the rostrum to tip of the telson) of brown shrimp was measured to the nearest millimeter (all shrimp and fish lengths given in this paper are total lengths). We identified cohorts visually from length-frequency charts and compared growth rates of the cohorts against a rate of 1 mm/d (Knudsen et al. 1977; Zimmerman et al., in press) as a check of our cohort identification. As an additional check of cohort parameters, we also fitted both normal and gamma distributions to the length-frequency data (Macdonald and Pitcher 1979; Macdonald 1987) with a computer algorithm, MIX (Macdonald and Green 1988). Mortality was estimated from changes in

density of brown shrimp in each cohort over the 2-week intervals.

Error for each mortality estimate was determined from sampling variability. The data were originally analyzed with a factorial analysis of variance (ANOVA) to test for effects of vegetation and location within the marsh during each sampling period (Zimmerman et al. 1984). We recalculated the ANOVAs for brown shrimp densities within a cohort, and determined the standard errors of cohort densities and mortality estimates from the error mean square in these analyses. These standard errors do not include error in identifying cohorts. Cohorts were most difficult to identify late in the spring (due to mixing with other cohorts and a broader size distribution), making mortality estimates during this time less dependable.

Predator exclusion experiment.—We placed predator-exclusion cages in the marsh on shallow nonvegetated bottom in 1987 (20 April to 21 May). The circular cages (1.5 m in diameter, 1 m in height) were constructed with fiberglass rings and galvanized hardware cloth covered by fiberglass screen (1-mm × 1.5-mm mesh). Cages were set at night and sunk about 15 cm into the mud bottom, after the area was swept clear with a seine. We removed enclosed animals with dip nets, and covered the cages with monofilament gill netting to exclude birds. We randomly assigned five cages as experimental cages and stocked them with 20 brown shrimp (30–35 mm); five other cages were not stocked and were designated as controls. After 2 weeks, we used the drop sampler to collect all animals from within the cages, and restocked randomly chosen cages with brown shrimp for a second 2-week period. We recorded temperature, salinity, and dissolved oxygen throughout the experiment at 30-min intervals with a Datasonde recorder suspended just above the substrate surface near the cages.

Stomach analyses of fishes collected in the marsh.—We examined stomach contents of fish from drop samples collected in the marsh from March 1982 through September 1984. Some abundant fish species were subsampled if their size or feeding behavior made them unlikely predators on penaeid shrimp. These species included the naked goby *Gobiosoma boscii*, gulf menhaden *Brevoortia patronus*, inland silverside *Menidia beryllina*, and anchovies *Anchoa* spp. All undamaged specimens of other species were dissected; thus the number of fish examined generally reflected the relative abundance of each species in the samples. In order to estimate fish densities, however, we

TABLE 1.—Summary data on experimental conditions and on sizes of fish predators and brown shrimp prey used in laboratory experiments to test effects of vegetation and prey density on predation rates. E is einsteins.

Predator	Date	Time (hours)	Total length (mm)		Light ($\mu\text{E} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$)
			Predator	Prey	
Pinfish	5 May 1983	1100–1130	37–59	12–15	45–180
	13 May 1983	1400–1430	41–69	11–16	40–130
Red drum	22 Jun 1983	1130–1200	43–48	12–19	20–110
Atlantic croaker	8 Apr 1983	1030–1100	44–80	8–12	60–120
Gulf killifish	1 Jul 1983	1530–1600	50–98	11–16	40–170
Southern flounder ^a	1 Jul 1984	1500–2100	82–115	25–32	0–119
	7 Aug 1984	1500–2100	110–160	25–32	0–365

^a Only one prey density (10/tank) was examined.

adjusted for variations in sampling intensity and included additional fish that were damaged when passing through the pump in the sampling process. We surveyed stomachs primarily for brown shrimp and white shrimp *Penaeus setiferus*, but also recorded frequency of occurrence for other food items, including fish, caridean shrimp, amphipods, tanaids, polychaetes, mysids, and copepods. Total length was measured for each predator and for shrimp prey whenever possible.

We estimated predator-related mortality of brown shrimp in the spring of 1982 by combining data on average stomach contents with fish densities. The model of Bajkov (1935) was modified and used to calculate the number of shrimp eaten per day as a function of the number of shrimp present in fish stomachs and the number of hours needed to completely evacuate the stomach.

Laboratory predation experiments.—We conducted predation experiments on the effect of vegetation and prey density in the laboratory. Predator and prey sizes and other experimental conditions are listed in Table 1. Both vegetation and prey density were examined in experiments with postlarval brown shrimp as prey and four species of fish predators: pinfish *Lagodon rhomboides*, Atlantic croaker *Micropogonias undulatus*, red drum *Sciaenops ocellatus*, and gulf killifish *Fundulus grandis*. We examined the effect of vegetation on feeding rates of southern flounder *Paralichthys lethostigma* with one density of juvenile brown shrimp as prey. Experimental animals were mainly collected in Galveston Bay with seines or trawls, but red drums were obtained from a hatchery operated by the Texas Parks and Wildlife Department in Palacios, Texas.

The glass tanks (0.18-m² bottom area) used in experiments had a substratum of washed beach sand. We filled tanks with seawater to a depth of

25 cm; ranges of salinity and temperature were 22–25‰ and 23–26°C. In vegetated treatments, we planted live *Spartina alterniflora* over the entire bottom in evenly distributed clumps of eight culms each. This vegetation density of 711 culms/m² is within the range that naturally occurs in Galveston salt marshes (Zimmerman et al. 1984). Before they were planted, *S. alterniflora* culms were stripped of decaying leaves and washed to remove epiphytic algae and associated fauna. Both holding and experimental tanks were in a laboratory with translucent skylights to allow the use of natural photoperiods. We conducted experiments during the day (Table 1), and measured light levels above the water's surface in μE (microeinsteins) $\cdot \text{s}^{-1} \cdot \text{m}^{-2}$ throughout each experiment with a LI-COR quantum meter (model LI-185B).

When we examined both vegetation and prey density, we used initial prey densities of 10 and 30 postlarvae per tank (56 and 167/m²) in combination with the presence or absence of vegetation. We used three replicate tanks per treatment combination and stocked three fish in each tank. Fish were held without food for 24 h before the experiment in 15-cm-diameter circular cages within the experimental tanks. We placed postlarval brown shrimp in the tanks 1 to 2 h before releasing fish from the cages. Fish were allowed to feed for 30 min, then removed from the tanks and dissected to determine the number of prey eaten.

The 30-min experimental duration was chosen because our preliminary feeding trials indicated that fish would begin feeding but not eat all available prey within this period. We also surveyed digestion rates to determine how long brown shrimp postlarvae would be identifiable in fish stomachs after ingestion. Fifty-one small fish, including individuals of all species used in the experiments, were fed individual brown shrimp (11–

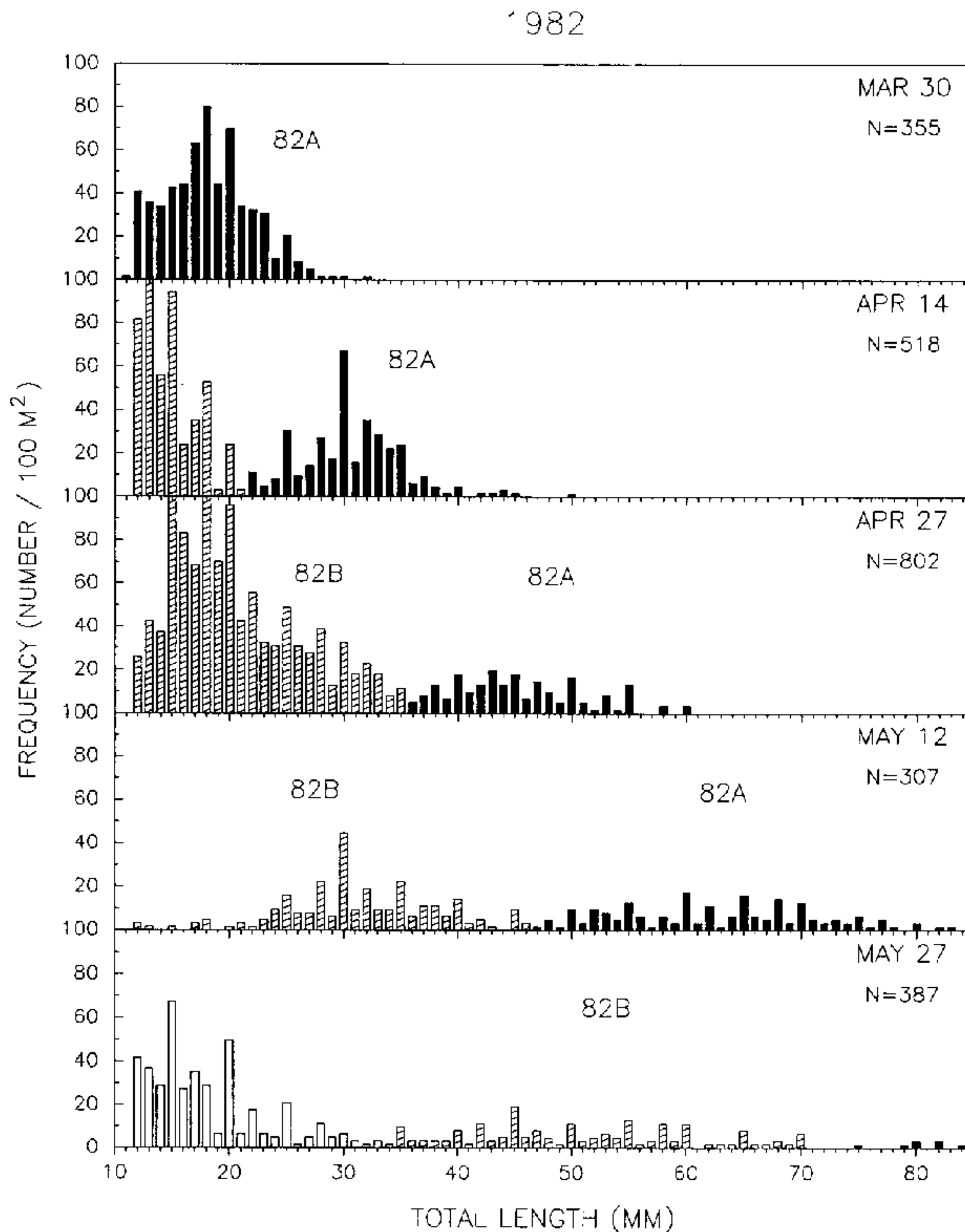


FIGURE 1.—Length frequencies of small brown shrimp at 2-week intervals in a Galveston Bay salt marsh (N = number sampled). Cohorts are identified by the shading of the bars (A = solid, B = hatched). Size ranges and means for each cohort are given in Table 2.

20 mm) and selected fish were dissected at 1-h intervals after ingestion. The time needed to digest a brown shrimp until it was no longer recognizable varied among species but was generally between 3 and 4 h. Temperatures during the digestion study ranged between 22 and 25°C and salinities between 25 and 27‰.

For each predation experiment, we placed subsamples of prey in additional tanks at the time of stocking to check mortality rates in the absence of predators. No mortality was observed. The number of brown shrimp eaten per fish during the 30-min feeding period was the observation in the ANOVAs, but replicate fish in each tank were considered subsamples, and among-tank variability

was used as the error term in significance tests. With pinfish, the entire experiment was repeated on a second day, and day was considered a blocking variable in the analysis.

We modified the experimental design for southern flounder because these fish were more difficult to obtain and less adaptable to laboratory conditions. The effect of *Spartina alterniflora* was examined with one predator per tank, and one density (10 prey per tank) of juvenile brown shrimp (25–32 mm). Prey were placed in the release cages instead of the predators, because feeding by southern flounder in preliminary studies was inhibited if the fish were confined to the relatively small cages before the experiment. After release of the

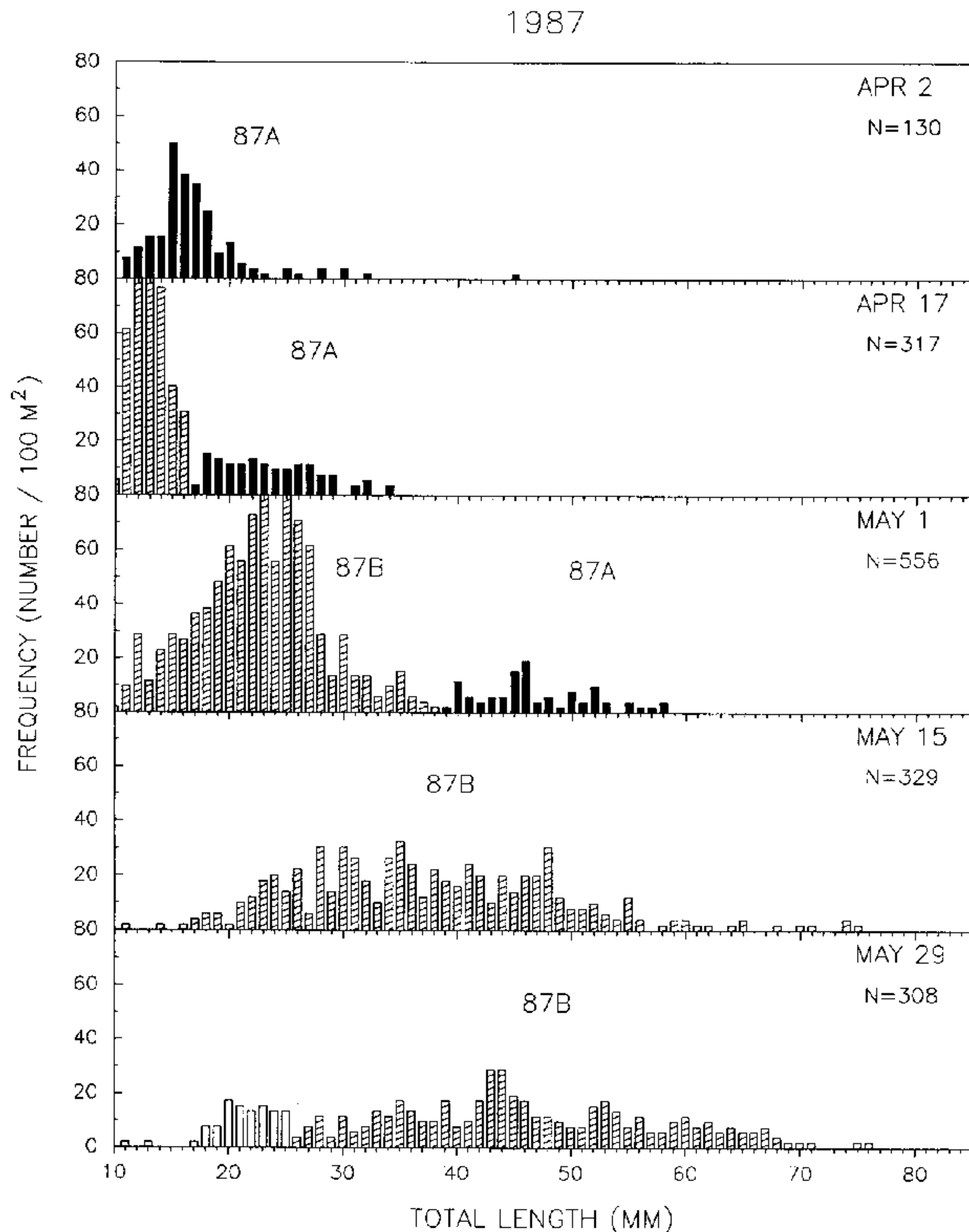


FIGURE 1.—Continued.

prey, fish were allowed to feed for 6 h before the experiment was ended. The number of brown shrimp eaten was determined by the number missing from the tank after this feeding period. We conducted the experiments with southern flounder on two occasions (Table 1) and tested 14 fish (seven for each treatment level). Day was used as a blocking variable in the ANOVA to test for a vegetation effect.

We also conducted two diel feeding-periodicity studies with southern flounder. In each of these studies, five fish were held individually in small containers under skylights. Temperatures were 24–26°C and salinities 24–25‰. Fish were fed brown shrimp ad libitum for a 12-h acclimation period

before the 3-d experimental period. We recorded the number of brown shrimp eaten every 3 h, and replaced missing prey. Predators of different sizes were used in the two studies, but prey size was adjusted for predator size. In preliminary feeding trials, the upper size limit of prey for southern flounder was not reached until brown shrimp were 33–50% of the total length of the predator. In the first feeding-periodicity study, southern flounder ranged from 91 to 98 mm (mean live weight, 7.5 g), and 25–30-mm brown shrimp were used as prey at a density of 73/m². In the second experiment, fish were 167–206 mm (mean live weight, 63.4 g) and brown shrimp (40–50 mm) were maintained at a density of 24/m².

TABLE 2.—Natural mortality of brown shrimp in a Galveston Bay salt marsh, 1982 and 1987, from cohort analyses based on the length-frequency data in Figure 1. The mean lengths of brown shrimp in cohorts were used to calculate growth estimates. Combined mortality for the two cohorts (82A and 82B) from 27 April to 12 May was 61%.

Cohort	Date	Total length (mm)		Growth (mm/d)	Density (number/100 m ²)	Mortality (SE)
		Range	Mean			
1982						
82A	30 Mar	11–32	18.2		603	
	14 Apr	22–50	30.8	0.8	350	42% (33)
	27 Apr	36–60	45.2	1.1	213	39% (20)
	12 May	47–83	62.8	1.2	210	1% (24)
82B	27 Apr	12–36	20.7		1,081	
	12 May	12–47	31.5	0.7	289	73% (20)
	27 May	34–70	50.7	1.3	194	33% ^a (19)
1987						
87A	2 Apr	11–32	16.8		248	
	17 Apr	17–34	23.6	0.5	152	39% (40)
	1 May	39–58	46.9	1.7	117	23% (29)
87B	1 May	10–38	22.7		952	
	15 May	11–75	37.5	1.0	666	30% (15)
	29 May	26–76	46.3	0.6	483	27% ^a (17)

^a Difficulty in delineating cohorts late in spring makes these mortality values less dependable (see Figure 1).

Results

Mortality Estimates

The first cohorts of brown shrimp arrived in the marsh during late March (Figure 1), and few brown shrimp were present in samples collected before this time. Cohorts identified visually (Table 2) from Figure 1 were used to estimate mortality, and cohort parameters from MIX analyses were similar (Table 3). Cohorts with a mean length less than

51 mm had mortalities ranging between 33% and 73% in 1982 (mean = 47%, SE = 8.9, $N = 4$) and between 23% and 39% in 1987 (mean = 30%, SE = 3.4, $N = 4$; Table 2). Mortalities consistently declined with duration in the marsh and with increased brown shrimp size. We were able to follow the first cohort identified in 1982 (82A) for the longest period of time. Estimated 2-week mortality was 42% as this cohort grew from 18.2 to 30.8 mm in mean length, and 39% as it grew from 30.8

TABLE 3.—Summary of MIX analyses of brown shrimp; both normal (n) and gamma (g) distributions were used to represent the length frequency data presented in Figure 1. Cohort size ranges were determined from intersection points between calculated distribution curves. Probability values from all chi-square tests of goodness of fit were less than 0.003. Size ranges, mean sizes, and growth rates are similar to the variables used in Table 2.

Cohort	Date	Total length (mm)				Growth (mm/d)	
		Range		Mean		n	g
		n	g	n	g		
1982							
82A	30 Mar	11–32	11–32	17.7	17.7	0.8	0.8
	14 Apr	20.5–50	21.5–50	29.8	30.2	1.1	1.1
	27 Apr	35–60	36–60	43.6	44.4	1.2	1.2
	12 May	44.5–83	49–83	61.3	62.9		
82B	27 Apr	12–35	12–36	19.7	20.1	0.7	0.8
	12 May	12–44.5	12–49	30.6	32.0	0.9	1.1
	27 May ^a	25–70	29–70	43.8	48.2		
1987							
87A	2 Apr	11–32	11–32	16.5	16.5	0.3	0.4
	17 Apr	16–34	16–34	21.5	21.8	1.7	1.8
	1 May	36–58	39–58	44.9	46.6		
87B	1 May	10–36	10–39	22.0	22.3	1.1	1.0
	15 May	11–75	11–75	37.0	37.0	0.5	0.5
	29 May	25–76	25–76	44.4	44.6		

^a Distribution was truncated at 71 mm.

TABLE 4.—Dominant fish predators on penaeid shrimp in a Galveston Bay salt marsh. Stomach contents of fish were analyzed to determine the frequency with which fish fed on *Penaeus* spp. The number of fish examined generally reflected the relative abundance of the species in drop samples. Spring data (March–May 1982) are a subset of the entire data set.

Species	Number of fish examined	Total length range (mm)	Number with food	Percent with shrimp ^a	Percent of all shrimp eaten ^b
Mar–May 1982					
Southern flounder	21	34–143	19	33.3	72.7
Gulf killifish	15	24–85	13	6.7	9.1
Pinfish	254	12–64	252	0.4	9.1
Spot	180	16–75	112	0.6	9.1
Mar 1982–Sep 1984					
Southern flounder	38	34–184	31	31.6	28.6
Spotted seatrout	116	11–135	95	15.5	46.4
Red drum	59	8–131	34	3.4	14.3
Gulf killifish	102	21–88	77	2.0	3.6
Pinfish	483	15–84	459	0.6	5.4
Spot	267	18–110	183	0.4	1.8

^a Percentage of fish examined that had eaten at least one *Penaeus* spp.

^b Percentage of the total number of *Penaeus* spp. found in all fish examined; this number was 11 shrimp for March–May 1982 and 56 shrimp through September 1984.

to 45.2 mm. As this cohort grew even larger, 2-week mortality was reduced to 1% (Table 2). This reduction occurred despite the increased probability of emigration from the marsh at these larger sizes, which would be measured as mortality in our estimates. During this time (27 April–12 May 1982) of low mortality for large brown shrimp, mortality of smaller animals in a second cohort (82B) was 73% (Table 2). The combined mortality estimate for brown shrimp of all sizes in the marsh from 27 April to 12 May was 61%, and mean mortality based on this estimate was 44% (SE = 6.0, $N = 4$) for 2-week periods in 1982.

Changes in mean shrimp length for cohorts corresponded to growth rates between 0.7 and 1.3 mm/d in 1982 and between 0.5 and 1.7 mm/d in 1987 (Table 2). Because a growth rate near 1 mm/d was assumed in identifying some of the cohorts, some of these rates may be biased, but growth rates from the MIX analyses were similar (Table 3).

Predator Exclusion Experiment

We used the percentage recovered of the 20 brown shrimp added to each of the experimental predator-exclusion cages to estimate potential survival in the absence of predators. Recoveries of brown shrimp from control cages were considered to be estimates of the number that had not been removed when the cages were set up, under the assumption that survival was not density dependent. Control cages, however, could not control for brown shrimp escape because they contained no experimental animals, nor could they com-

pletely control for brown shrimp entering cages because the controls may not have attracted animals in the same manner as experimental cages. For these reasons, breaches or openings in the cage walls could seriously affect estimates of survival. Three of the 10 experimental cages and two of the 10 controls had burrows under the cage walls at the time of recovery (apparently due to the blue crab *Callinectes sapidus*), and these cage data were eliminated from the analysis.

The initial size range for experimental brown shrimp was 30–35 mm, and only individuals longer than 35 mm were counted as survivors. After 2 weeks, either 19 or 20 brown shrimp were recovered from each of the seven experimental cages, and the mean mortality rate was 2.8%. Only one brown shrimp was recovered from the eight controls. Daily growth estimates from the experimental cages ranged from 0.6 to 1.6 mm/d, averaging 1.2 mm/d. Estimated growth rates from the cohort analysis during this period (20 April–21 May 1987) were 1.0 and 1.7 mm/d (Table 2).

During the caging study, water temperatures were 20–34°C and salinities 29–34‰. Dissolved oxygen generally reached a maximum in the afternoon, frequently above 11 mg/L, and a minimum just before sunrise. On three nights during the experiment, hypoxic conditions were recorded (below 2.0 mg/L), and the lowest dissolved oxygen reading was 1.5 mg/L.

Stomach Analyses of Fishes Collected in the Marsh

Southern flounder was the dominant fish predator on small brown shrimp in spring. From March

through May 1982, 33% of the 21 southern flounder examined had been eating brown shrimp (Table 4). Of the 11 penaeid shrimp found in all fish stomachs during this period, 8 were eaten by southern flounder. Brown shrimp were also found, although infrequently, in stomachs of pinfish, spot *Leiostomus xanthurus*, and gulf killifish. Only 14 Atlantic croakers were collected, and no penaeid shrimp were observed in their stomachs. However, similar stomach analyses of small fishes in Lavaca Bay, Texas, indicated that Atlantic croaker are minor predators on penaeid postlarvae (Minello et al. 1989).

Southern flounder feeding on brown shrimp in the spring of 1982 ranged in size from 85 mm to 143 mm (mean = 89.1 mm, SE = 9.8, $N = 7$), and their brown shrimp prey ranged from 14 mm to 40 mm (mean = 29.5 mm, SE = 3.0, $N = 8$). The relative size of the prey in relation to the predator ranged from 17% to 47% (mean = 34%, SE = 4.0, $N = 8$).

We used the average density of southern flounder in the five sampling periods in spring 1982 (mean = 7.1/100 m²; SE = 1.8; $N = 5$) and the incidence of feeding (8 brown shrimp in 21 southern flounder examined; Table 4) to estimate that

the population of southern flounder in 100 m² of marsh would have 2.8 brown shrimp in their stomachs at any time. All other fish predators combined in 100 m² were estimated to have 1.1 brown shrimp in their stomachs. For ambush predators such as the southern flounder, which feed on relatively large prey, a linear function adequately represents gastric emptying (Jobling 1986, 1987). We assumed that southern flounder feed continuously, as suggested by our laboratory feeding studies (discussed below), and that their evacuation time is 4 h. Under these conditions, we used the model of Bajkov (1935) to estimate that 17 shrimp would be eaten daily by the population of southern flounder in 100 m² of the marsh.

Postlarvae and juveniles of both brown shrimp and white shrimp occur in the marsh throughout the summer and autumn, although brown shrimp numbers are reduced during these periods (Zimmerman and Minello 1984). Stomach analyses of fish collected throughout the year (between March 1982 and September 1984), indicated that spotted seatrout *Cynoscion nebulosus* were frequent predators on penaeid shrimp (Table 4). In addition, red drums were responsible for over 14% of all penaeid shrimp eaten, but only two of the 59 fish

TABLE 5.—Dominant prey of shrimp predators in vegetated (VG) and nonvegetated (NV) samples from a Galveston Bay salt marsh. Decimal fractions are percentages of fish examined containing each type of prey. Only fish that had eaten penaeid shrimp are included. Spring data (March–May) are a subset of the entire data set.

Number of fish examined (N) and prey type	Southern flounder		Gulf killifish		Pinfish		Spot		Spotted seatrout		Red drum	
	VG	NV	VG	NV	VG	NV	VG	NV	VG	NV	VG	NV
Mar–May, 1982–1984												
N	16	14	31	0	393	61	43	215	0	0	0	0
Penaeid shrimp	43.8	7.1	3.2		0.3	1.6	0.0	0.5				
Amphipods	0.0	28.6	29.0		48.1	68.9	25.6	22.3				
Tanaids	6.3	7.1	16.1		21.1	29.5	16.3	16.3				
Mysids	0.0	21.4	0.0		3.1	0.0	0.0	0.0				
Copepods	0.0	0.0	0.0		12.5	6.6	9.3	7.4				
Isopods	6.3	0.0	0.0		1.5	0.0	9.3	1.9				
Blue crabs	6.3	0.0	0.0		0.0	0.0	0.0	0.0				
Grass shrimp	12.5	14.3	0.0		0.3	0.0	0.0	0.0				
Polychaetes	6.3	0.0	6.5		8.7	13.1	7.0	24.7				
Fish	37.5	21.4	3.2		0.3	1.6	4.7	1.4				
Plant material	6.3	0.0	25.8		23.4	50.8	14.0	20.0				
Mar 1982–Sep 1984												
N	21	17	102	0	402	81	43	224	106	10	25	34
Penaeid shrimp	42.8	17.6	2.0		0.5	1.2	0.0	0.4	15.0	20.0	8.0	0.0
Amphipods	0.0	23.5	22.5		74.1	55.6	27.9	23.7	25.4	20.0	32.0	20.5
Tanaids	4.8	5.9	6.9		46.0	23.5	18.6	12.5	14.1	0.0	28.0	0.0
Mysids	0.0	29.4	2.0		3.2	1.2	0.0	0.0	57.5	70.0	12.0	8.8
Copepods	0.0	0.0	0.0		12.7	4.9	9.3	7.6	3.8	0.0	4.0	2.9
Isopods	4.8	0.0	0.0		2.0	0.0	9.3	1.8	0.0	10.0	0.0	0.0
Blue crabs	9.5	0.0	1.0		0.2	0.0	0.0	0.0	0.0	0.0	4.0	0.0
Grass shrimp	9.5	12.9	2.0		0.2	0.0	0.0	0.0	5.7	0.0	0.0	0.0
Polychaetes	4.8	0.0	5.9		9.7	12.3	7.0	24.6	0.9	0.0	0.0	0.0
Fish	28.5	23.5	2.0		0.7	1.2	4.7	1.3	0.9	20.0	0.0	11.7
Plant material	14.2	0.0	28.4		26.6	55.6	14.0	19.6	16.9	10.0	12.0	8.8

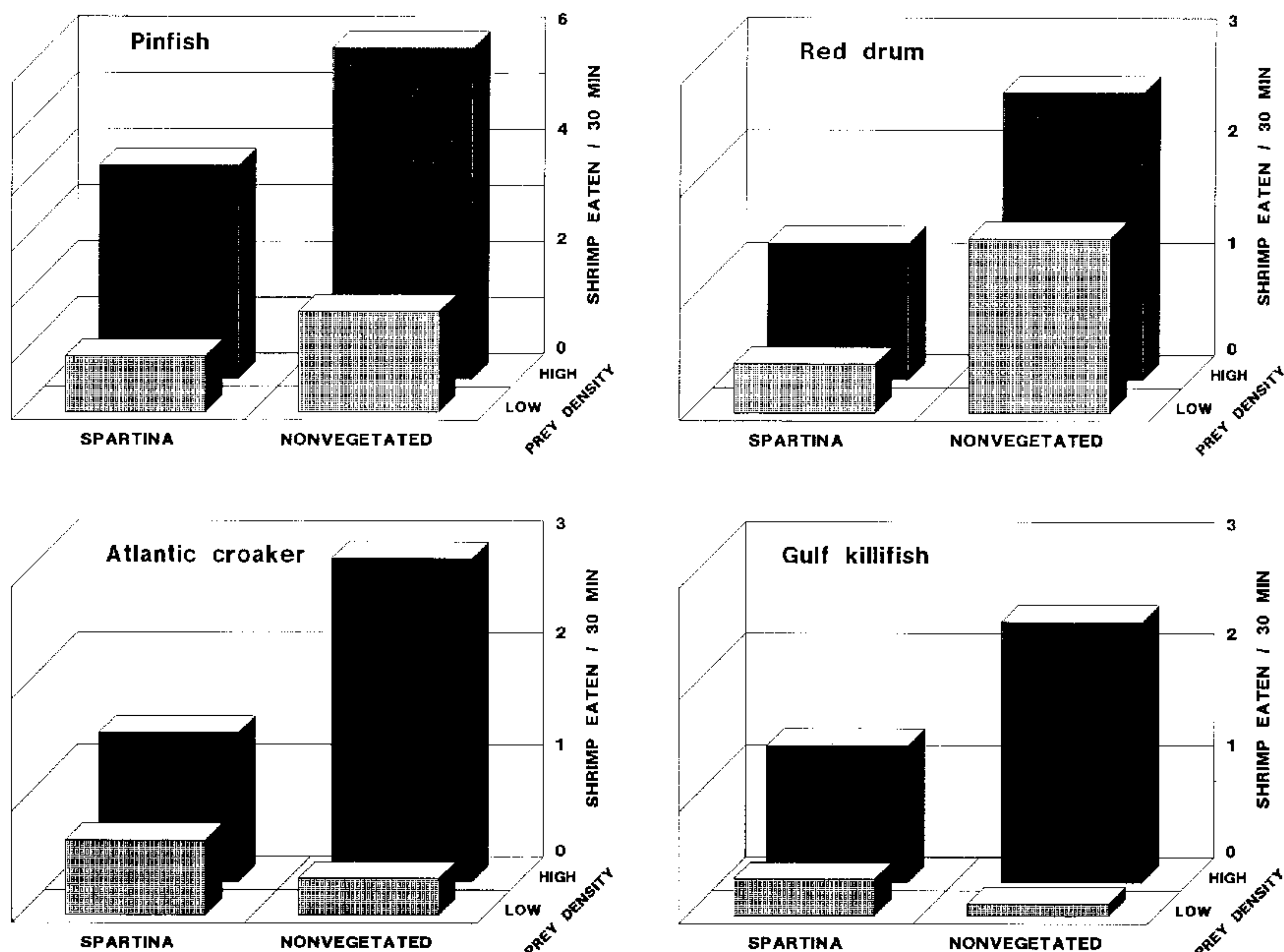


FIGURE 2.—Effect of vegetation (*Spartina*) and prey density on mean feeding rates of four fish species. Postlarval brown shrimp were used as prey at two densities, 56 and 167/m². Tests of statistical significance are listed in Table 6.

examined had eaten shrimp (those two fish contained eight shrimp). Predation by spotted seatrout and red drum occurred mainly from late summer through winter when the young of these species were abundant in the marsh (Zimmerman and Minello 1984).

Young southern flounder, found in the marsh mostly in spring, appeared to be equally abundant in vegetated and nonvegetated habitats. Selection of penaeid shrimp as prey was related to the habitat in which the fish was caught. From March through May in 1982, 1983, and 1984, 44% of southern flounder collected in vegetated samples had eaten brown shrimp whereas only 7% of the southern flounder from nonvegetated samples had eaten brown shrimp (Table 5). Despite the small sample size, a *G*-test of independence indicated significant association between the presence of penaeid shrimp in stomachs of southern flounder and the presence of vegetation in a sample ($G_{adj} = 5.22$, $P < 0.025$; Sokal and Rohlf 1981). Southern flounder in both habitats fed upon fish and grass shrimp *Palaemonetes pugio*, whereas am-

phipods and mysids were eaten only by fish collected in nonvegetated samples.

In addition to small numbers of penaeid shrimp, pinfish, spot, and gulf killifish frequently fed upon peracarid crustaceans in spring (Table 5). Pinfish generally occurred in vegetated samples (86%) and fed on amphipods, tanaids, and plant material. Juvenile spot were mainly collected over nonvegetated bottom (83%), and about 31% of these fish contained no food; the most frequently eaten prey items, however, were amphipods, tanaids, and polychaetes. All gulf killifish were collected in samples with *Spartina alterniflora*, and this resident marsh predator fed mainly upon amphipods, tanaids, and insects.

Laboratory Predation Experiments

The presence of *Spartina alterniflora* significantly reduced feeding rates of southern flounder by 53%, from a mean of 4.1 brown shrimp per fish over 6 h in nonvegetated tanks to 2.0 brown shrimp per fish in vegetated tanks ($F = 6.1$, $df = 1, 11$, $P = 0.03$). Vegetation also had significant

TABLE 6.—Analysis of variance results from laboratory predator–prey experiments. The number of brown shrimp postlarvae eaten per fish was the observation, and among-tank error was used to test for main effects and interactions. P^* is the probability from the same analysis when the percentage of shrimp eaten was the observation. Additional information on experiments is given in Table 1.

Source of variation	df	Sum of squares	<i>F</i>	<i>P</i>	<i>P*</i>
Pinfish					
Total	71	1,031.11			
Vegetation	1	37.56	6.92	0.016	0.003
Prey density	1	213.56	39.35	<0.001	0.31
Vegetation × density	1	8.00	1.47	0.24	0.86
Day (block)	1	174.22	32.10	<0.001	<0.001
Error (among tanks)	19	103.11	0.53	0.94	0.97
Error (within tanks)	48	494.67			
Red drum					
Total	35	56.89			
Vegetation	1	13.44	14.24	0.005	0.003
Prey density	1	7.11	7.53	0.025	0.078
Vegetation × density	1	0.11	0.12	0.74	0.11
Error (among tanks)	8	7.56	0.79	0.62	0.79
Error (within tanks)	24	28.67			
Atlantic croaker					
Total	35	247.64			
Vegetation	1	3.36	0.95	0.36	0.78
Prey density	1	23.36	6.62	0.033	0.54
Vegetation × density	1	8.03	2.28	0.17	0.22
Error (among tanks)	8	28.22	0.46	0.87	0.78
Error (within tanks)	24	184.67			
Gulf killifish					
Total	35	110.00			
Vegetation	1	1.78	0.36	0.57	0.81
Prey density	1	21.78	4.38	0.070	0.25
Vegetation × density	1	4.00	0.80	0.40	0.35
Error (among tanks)	8	39.78	2.80	0.024	0.028
Error (within tanks)	24	42.67			

effects on feeding rates of pinfish (overall mean reduction of 44%) and red drums (62% reduction; Figure 2; Table 6). At high prey densities, mean feeding rates in vegetation for both Atlantic croakers and gulf killifish were about one-half those in nonvegetated tanks, but at low prey densities, mean feeding rates were higher within the vegetation. Lack of the expected significant interaction term in the ANOVA (Table 6) may have been partially due to the low incidence of feeding by these predators. Of the 36 fish in each experiment, only 39% of the gulf killifish and 47% of the Atlantic croakers fed, compared to 70–72% of the fish in pinfish and red drum experiments. However, an examination of the among-tank error terms indicated that the power of the Atlantic croaker analysis was similar to that for pinfish and red drum. Among-tank error in these three analyses ranged from 10% to 13% of the total. In the experiment with gulf killifish, among-tank error (36% of total) was significantly larger than within-tank error (Table 6), and the power to detect statistical differences for main effects and interaction was low.

A decrease in initial prey density from 30 to 10 postlarvae per tank (167 to 56/m²) significantly reduced feeding rates of pinfish (74% mean reduction for vegetated and nonvegetated treatments combined), red drums (47% reduction), and Atlantic croakers (76% reduction; Figure 2; Table 6). Mean feeding rates of gulf killifish were reduced by 89%, but the effect of prey density was not significant at the 0.05 level in the ANOVA due to a large within-tank error term. Predation rates were approximately proportional to prey densities (Figure 2), and density effects were therefore not statistically significant when proportional mortality of brown shrimp was used in the ANOVAs (Table 6). The use of proportional data did not appear to alter the significance of vegetation effects in the analyses.

In diel periodicity studies, southern flounder fed on shrimp throughout the day and night (Figure 3). Although mean predation rates were highest during afternoon hours, variability among individual fishes prevented the statistical detection of any temporal differences. Despite overall differ-

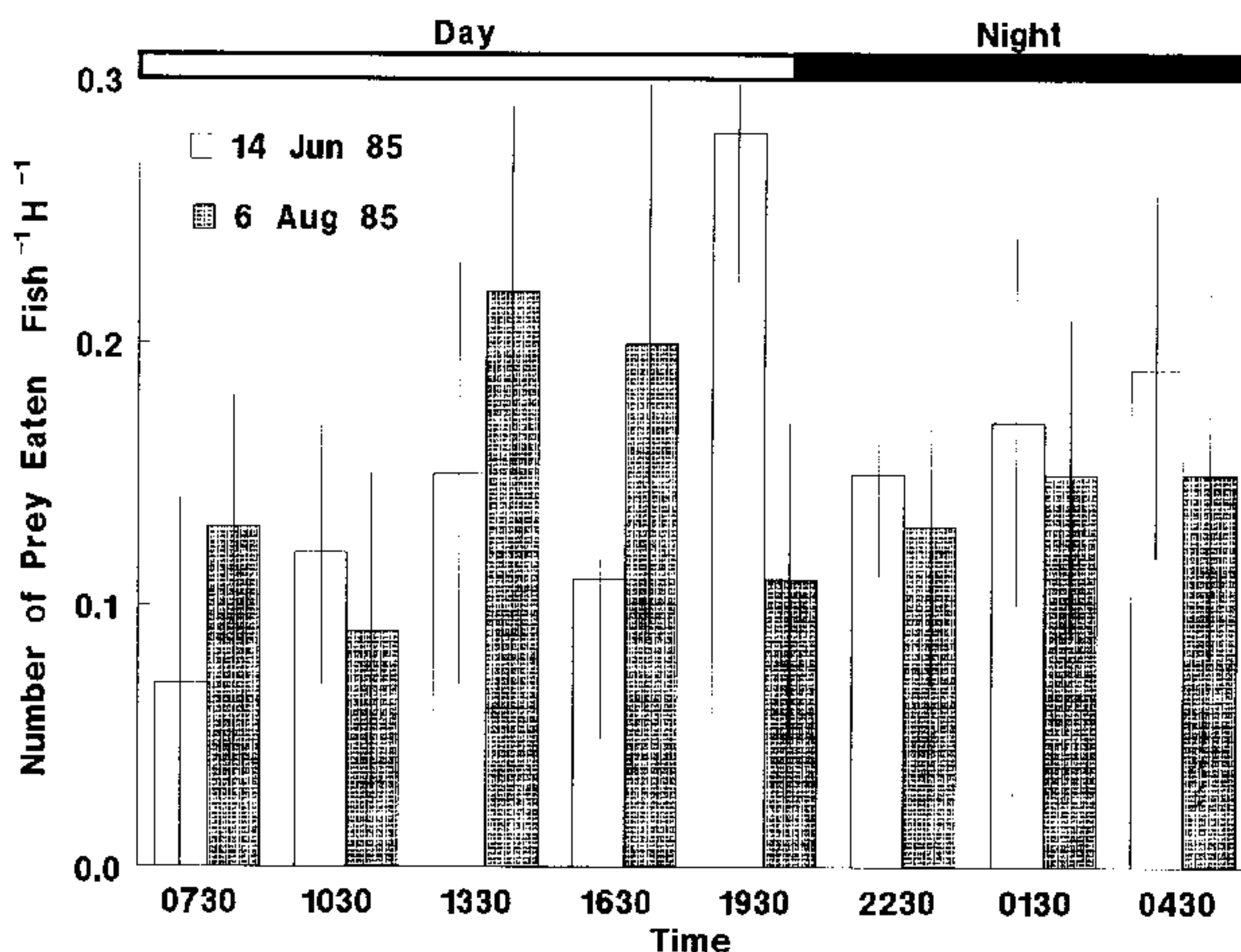


FIGURE 3.—Diel periodicity of feeding by southern flounder on juvenile brown shrimp. The time of each observation represents the center of a 3-h feeding period. Data for each fish were averaged over the 3-d experiments (the date of day 1 is shown), and the mean feeding rates (vertical bars) and SEs (vertical lines) are from replicate fish ($N = 5$).

ences in predator and prey size, the mean number of brown shrimp eaten per fish per day was similar in the two feeding-periodicity studies. The smaller fish ate 3.8 brown shrimp/d ($SE = 0.94$)—about 7.6% of their own live weights—and the large fish ate 3.6 brown shrimp/d ($SE = 1.26$)—4.0% of their weights.

Discussion

Magnitude of Shrimp Mortality in Estuaries

If mortality of young brown shrimp in estuarine nurseries is large and highly variable, ecological relationships that regulate this mortality can also regulate recruitment to the fishery. Few attempts have been made to estimate mortality of young shrimp in estuaries. Mark-recapture techniques, which are frequently used for larger individuals, have been unsuccessful because smaller shrimp are difficult to mark (Klima 1965; Farmer 1981). Cohort analyses, in which populations are followed through time by sequential examination of length frequencies (Pauly et al. 1984), are potentially useful because brown shrimp postlarvae enter estuaries in waves (Baxter and Renfro 1967), and cohorts can be identified in shallow nursery areas. This technique requires accurate estimates of animal densities over a wide size range in a population, and the drop-sampling methods developed by Zimmerman et al. (1984) have dra-

matically improved our ability to measure densities of brown shrimp in shallow estuarine habitats. Tracking a population is possible in these nursery habitats because the ontogenetic migration of brown shrimp appears to be interrupted while they grow into large juveniles.

Mortality of young brown shrimp in estuaries is relatively large in relation to mortality at later life history stages. Our estimates of mortality for 2-week periods in a Galveston Bay salt marsh ranged from 23 to 61% in the springs of 1982 and 1987. Other estimates of mortality (adjusted to 2-week rates) in estuaries have been made by McCoy (1972) for subadult *Penaeus aztecus* (52%) and by Edwards (1977) for juvenile *Penaeus vannamei* (65%). In contrast, Rothschild and Brunenmeister (1984) concluded that the best estimates of annual instantaneous natural mortality for subadult and adult brown shrimp ranged from 1.0 to 3.0, corresponding to actual 2-week mortalities of 4–11%.

Our data suggest that mortality of brown shrimp can vary substantially over years and throughout the spring within a year. Size also appears to be important, and mortality of different cohorts during the same sampling period (27 April–12 May 1982) varied from 73% for small individuals to 1% for large juveniles. In addition, we would expect mortality to change with habitat type and location. Mortality in these nurseries, therefore,

appears to be large and highly variable, making the estuarine period in the brown shrimp life cycle critical in the regulation of recruitment to the fishery.

Relative Importance of Physical and Biological Controls

It is less important to determine the exact magnitude of mortality in estuaries than to understand the biotic and abiotic factors that regulate mortality. Natural mortality of young brown shrimp in estuaries may be affected by inadequate food, disease, physical conditions, or predation. Research on food requirements (Gleason and Zimmerman 1984) and the natural occurrence of parasites and disease (Overstreet 1973; Couch 1978; Fontaine 1985) suggests that these factors do not directly result in mortality of brown shrimp.

Evidence about the importance of the physical environment in regulating mortality is conflicting. Juvenile brown shrimp have been collected in waters with temperatures ranging from 2 to 38°C and salinities from 0 to 45‰ (Zein-Eldin and Renaud 1986). In the laboratory, brown shrimp postlarvae survived 1-d exposures to temperatures as low as 7°C if salinity was above 10‰, and little mortality was observed during 28-d exposures unless temperature and salinity were simultaneously low (below 15°C and 10‰) or the temperature was above 35°C (Zein-Eldin and Aldrich 1965). Juvenile brown shrimp can also survive in the laboratory at dissolved oxygen concentrations below 1 mg/L (Kramer 1975), and oxygen concentrations in our field cages dropped to 1.5 mg/L for short periods without any apparent effect on mortality.

Catastrophic mortality of organisms, including brown shrimp, has been documented in estuaries due to severe cold fronts in early spring (Gunter 1941; Gunter and Hildebrand 1951; Dahlberg and Smith 1970) and to persistent hypoxic conditions in summer (Gunter 1942; May 1973; Turner and Allen 1982; Turner et al. 1987). During most of the spring, however, when the major waves of brown shrimp postlarvae enter the estuaries of the northern Gulf of Mexico, the physical environment does not appear to be a major cause of mortality.

Results from our predator-exclusion experiment support the hypothesis that predation is a major factor regulating brown shrimp mortality in estuaries. From seven predator-exclusion cages, our estimate of 2-week mortality was about 3%

from 20 April to 21 May 1987. The drop-sampling technique used to harvest the cages has a recovery failure of around 2% (Zimmerman et al. 1984), suggesting that mortality in the absence of predators was close to zero. During the same time, 2-week mortalities in the marsh were estimated at 23% and 30% from cohort analyses.

Fish Predation and Brown Shrimp Mortality

The effect of a predatory species on a population depends on both the frequency with which the predator feeds on a particular prey and the relative abundance of that predator. In spring, southern flounder was the dominant predator on brown shrimp (over 70% of the shrimp eaten), but pinfish, spot, and gulf killifish also ate brown shrimp. Abundant fish, such as pinfish, are potentially important predators because a small increase in selection for brown shrimp would result in a large effect on mortality. Spotted seatrout and red drums also ate postlarvae and juveniles of both brown shrimp and white shrimp in relatively large numbers, but these predators were present in the marsh mainly in summer and autumn.

In an effort to estimate whether predation by fish could be responsible for observed shrimp mortality, we compared our estimates of mortality from cohort analysis with estimates of predator-related mortality in the spring of 1982. Using a 2-week average mortality of 44%, we estimated that 31 shrimp would be lost daily from a 100-m² area of salt marsh (4.0% daily mortality; mean shrimp density during five sampling periods was 765/100 m²). Our estimate of predator-related mortality from stomach contents of southern flounder was 17 brown shrimp eaten daily in the same area of marsh, and predation mortality would be even closer to our estimate of 31 shrimp if other shrimp predators were included. If we assumed that southern flounder fed solely on brown shrimp, we could also calculate their daily intake from a food requirement of about 3.8 brown shrimp per fish per day, which we obtained from our laboratory feeding-periodicity studies. Under these conditions, the density of southern flounder in 100 m² of the marsh could be responsible for the mortality of 27 brown shrimp per day. Despite the several sources of error in the calculations, these comparisons suggest that southern flounder and other fish predators are responsible for much of the spring mortality of brown shrimp in the marsh.

The importance of southern flounder in regulating brown shrimp mortality was also suggested

by a comparison of the two years studied. Mean spring mortality appeared lower in 1987 (30%) than in 1982 (44%), although the difference was not significant in a *t*-test at the 5% level ($P = 0.09$, 6 df). This apparent reduction in mortality coincided with reduced densities of southern flounder in 1987 (mean = 1.9/100 m²; SE = 0.6; $N = 5$ sampling periods) compared with 1982 (mean = 7.1/100 m²; SE = 1.8; $N = 5$).

Environmental Interactions with Predation

Predation rates can be affected by many factors. Our laboratory experiments showed that, even in the absence of alternative prey, the presence of *Spartina alterniflora* reduced predation rates of southern flounder, pinfish, and red drums. Increased brown shrimp density generally increased predation rates. Other experiments have shown that predation rates on brown shrimp are affected by vegetative structure (Minello and Zimmerman 1983, 1985), substrate type (Minello and Zimmerman 1984; Minello et al. 1987), and water clarity (Minello et al. 1987). Prey selection appears to be regulated by the same habitat characteristics that affect overall predation rates, which should be expected if we assume that the protective value of habitats is not the same for all prey organisms. Prey density must also regulate selection, and this was apparent from the significant association between prey selection by southern flounder in the marsh and the presence of vegetation. Increased selection for brown shrimp in the *Spartina alterniflora* habitat coincided with brown shrimp densities ranging between 4.5 and 10.6 times the densities on nonvegetated bottom (Zimmerman et al. 1984).

If predation by fishes is an important regulator of mortality of juvenile brown shrimp, water levels in the marsh become critical because they regulate access to vegetation and also can control brown shrimp densities. Some fish predators of penaeid shrimp, including spotted seatrout, pinfish, and gulf killifish, select for *Spartina alterniflora* habitat over nonvegetated bottom, but southern flounder does not appear to select for either habitat (Zimmerman and Minello 1984). Therefore, mortality due to predation by southern flounder should be relatively low when brown shrimp are concentrated in vegetation at high water levels, which generally occur in marshes of the northern Gulf in spring (Hicks et al. 1983). As water levels fall, protective vegetation becomes inaccessible, both predator and prey densities increase on subtidal

bottom, and brown shrimp mortality should increase.

Physical conditions and the type and quantity of food available regulate growth of brown shrimp (Zein-Eldin and Aldrich 1965; Gleason and Zimmerman 1984; Gleason and Wellington 1988; Zimmerman et al., in press), and growth rates may interact with predator-related mortality. Our preliminary feeding studies in the laboratory suggest that southern flounder feed on brown shrimp only until they reach 33% to 50% of the total length of the predator. Brown shrimp in stomachs of southern flounder from the marsh ranged from 17% to 47% (mean = 34%) of the length of the fish. Rapid growth of brown shrimp in relation to growth of southern flounder should reduce the time these prey are of a vulnerable size. Although variable, growth rates of 1 mm/d are frequently reported for juvenile brown shrimp (Knudsen et al. 1977; Zimmerman et al., in press). In order to maintain a constant predator : prey size ratio of 3:1 in total length, southern flounder would have to grow at a rate of 3 mm/d. Length-frequency data for young-of-the-year southern flounder in south Texas suggest spring growth rates around 0.7 mm/d (Stokes 1977), indicating that brown shrimp can grow beyond the optimal prey size of these predators. Environmental conditions that affect shrimp growth could regulate mortality through such a mechanism.

If predation pressure is reduced as brown shrimp grow, mortality rates of larger juveniles should be relatively low. Our length-frequency data from the marsh suggest that mortality decreased as the mean length of brown shrimp in a cohort increased. In 1982 (27 April–12 May), mortality for brown shrimp with a mean total length between 20.7 and 31.5 mm (cohort 82B) was estimated at 73%, whereas mortality for individuals between 45.2 and 62.8 mm (cohort 82A) was only 1%. Southern flounder in the marsh during these sampling periods had a mean total length of 86 mm (SE = 7.9, $N = 13$). If these fish were unable to feed on shrimp larger than 43 mm (50% of mean predator length), predation by southern flounder on shrimp in cohort 82A would have been low.

Seasonal changes in factors affecting shrimp mortality should make survival of brown shrimp postlarvae in estuarine nurseries dependent upon the time of their arrival each spring. Early arrival will increase the probability of death from catastrophic physical conditions such as freezes combined with low water. Mortality due to fish pred-

ators will depend upon characteristics of the predator populations, but low water levels in early spring (Zimmerman et al. 1984) should increase predation by increasing prey densities on nonvegetated bottom. Low temperatures and slow growth will also keep shrimp vulnerable to predators for a longer period of time. Midspring arrivals should have the advantage of warmer temperatures for faster growth and little chance of catastrophic physical conditions. More consistently high water levels will also reduce prey densities on nonvegetated bottom and provide access to protective vegetation. In late spring and early summer, water levels decrease again, increasing brown shrimp densities on nonvegetated bottom. The presence of large fish predators and the reduced abundance of benthic infauna and epifauna (Potts 1978; Flint 1985), which serve as alternative prey for smaller fish predators, may increase predation pressure on shrimp at this time of the year. The positive effect of warmer temperatures on growth may also be checked by depleted food resources for brown shrimp (Zimmerman et al., in press).

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